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TEMPORAL CHARACTERISTICS OF GROOMING IN AN OPEN FIELD IN TWO STRAINS OF RATS

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ABSTRACT: The temporal characteristics of grooming in an open field were studied in rats from two different genotypes (NR, brown Norway rats bred from an original wild stock and KM, Krushinsky-Molodkina albino rats selectively bred for audiogenic seizure susceptibility). The measures of grooming recorded were time of onset of any grooming activity, duration and number of grooming episodes and total time spent grooming during successive 3-min intervals over a total 12-min period. The results demonstrated that grooming episodes of different durations displayed different features across the course the test. Grooming was minimal in the first minutes of the test and the longest grooming episodes were observed after the sixth minute in most of the rats. The number and proportion of prolonged episodes (over 21 s in duration) increased over time. Short-duration episodes (1-3 s) were not connected with the specific stage of the test and/or the decrease in locomotion. The scores of grooming duration were higher in NR in comparison to the KM rats. No significant effects were found for strain and sex for total numbers of grooming episodes.

Grooming behavior in rodents, and particularly in the rat, is often observed as an expression of stress in novel, dangerous or conflict situations (Barnett, 1975; Bindra & Spinner, 1958; Cohen & Price, 1979; Fentress, 1973; Jolles, Rompa-Barendregt, J. & Gispen, W. H., 1979). It has also been identified as a displacement activity (Delius, 1970; Krushinsky & Semiokhina, 1973; Tinbergen, 1952). Although grooming behavior has been studied extensively (see Berridge, 1990), there are relatively few studies of grooming on the open field, and in such studies (e.g. Doyle & Yole, 1959; Ivinskis, 1968; O'Kelly, 1949) observations were typically made for only two or three minutes. Prolonged exposure to the open field induces habituation to novel or fear-inducing factors, and so their stressful effects likely decrease over the course of time. Observations indicate that there is a trend toward a

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high level of grooming behavior with prolonged exposure to the open field.

In order to understand what mediates the grooming response, we measured the time of onset and duration of grooming episodes, as well as the relationship of grooming with other behaviors on the open field across a 12-min period. The behavior of two stocks of rats was compared: brown Norway rats, with high grooming scores and a rich behavioral repertoire; and rats from the Krushinsky-Molodkina stock (albino rats selectively bred for susceptibility to audiogenic seizures) with poor grooming scores (Pleskacheva, Sotskaya, Krushinsky et al., 1990). Shtemberg (1982) and Pleskacheva (1985) have reported an increase in grooming duration in the brown Norway rat after the third minute of observation in the open field. And Pleskacheva et al. (1990) observed no decrease in time spent grooming by Krushinsky-Molodkina rats during a second open-field trial.

METHOD

Subjects

Two strains of rats were studied. Albino rats from the Krushinsky-Molodkina (KM) stock and brown Norway rats (NR). The Norway rats were from the tenth generation of an original wild stock. The albino rats were selectively bred for audiogenic seizure susceptibility; they exhibited clonic and tonic seizures within 1.5 min of exposure to the sound of a 120db electric bell (Krushinsky, Molodkina, Fless, et al., 1970; Semiokhina, Fedotova & Kuznetsova, 1993). In comparison with commercially outbred albino rats that do not show audiogenic seizures, serotonin and norepinephrine levels are reduced in this stock (Sergienko & Loginova, 1983), cortical acetylcholinesterase activity is high (Eremeev, 1969), and there are deficits in the binding capacity of GABA and benzodiazepine receptors in the cerebellum, neocortex and brain stem (Zhulin & Pleskacheva, 1991).

Twenty-seven females and 27 males of the KM strain, ranging in weight from 200-230 gm and 300-350 gm respectively, and 26 females and 26 males of the NR strain, ranging in weight from 200-250 gm and 300-400 gm respectively, were observed. Both stocks ranged in age from 4 to 8 months, were experimentally naive, had received no previous handling, and had not been bred. Rats were weaned when one month old. Three to five rats (usually from the same litter) of the same sex, age and stock were housed in plastic cages (40 x 35 x 16 cm) in a

colony room maintained on a 10:14 light/dark cycle and at 20 degrees Celsius. They were fed on a diet of grain, bread, boiled and raw meat, cabbage and carrot. Food and water were freely available.

Apparatus

The animals were tested in a circular open field, 100 cms in diameter. The 50 cm high walls were made from light tin and the floor was covered with light brown linoleum, divided into 16 sections by black grids (22x22 cm): the 4 central squares were of equal area, the other 12 segments were somewhat smaller. The field was illuminated by a 200 watt bulb, centered above the apparatus, 50 cm above the floor. Noise in the experimental room was from 30-40 db.

Procedure

The animals were tested during the light phase of their L/D cycle, between 10 a.m. and 3 p.m. When removed from the home cage a rat was placed on the experimenter's arm and transferred to the centre of the open field where it was observed for 12 minutes. Each rat was tested once. The apparatus was cleaned with a very weak soapy solution between subjects.

The following measures of grooming were recorded using a stopwatch and checklist: time of onset of any grooming activity (washing muzzle and head area behind the ears, body licking, anogenital and tail grooming, scratching); duration of each grooming episode (minor interruptions of 1-2 s were ignored); number of grooming episodes; and total time spent grooming during successive 3-min intervals and for the entire 12-min observation period. The observer also recorded the number of floor squares crossed; rearing (number of vertical postures); urination (presence or absence) and defecation (number of fecal boli).

RESULTS

General characteristics of rat grooming

Figure 1 shows the mean time spent grooming by males and females of both strains of rats across successive 3-min blocks of the 12-min observation period. With the exception of one KM rat, all rats were observed to groom during the open-field test. Although both

strains exhibited distinctive grooming activities, which will be described below, several features of the grooming patterns were similar in both strains of rats. For example, no grooming occurred during the first test minute; grooming began to appear during the 2nd - 3rd minutes, and increased as time went on. There were considerable individual differences in the number of grooming episodes and, particularly, in the duration of these episodes. These ranged from 1-2 sec of head washing movements to protracted reactions (up to 2.5 min) that included the whole sequence of grooming acts. There was a significant increase in grooming duration in the course of the 12-min open field test. A 2-way repeated measures ANOVA (time by sex) showed this finding for both strains: $F(3,200) = 11.84$, $p<0.001$ for Norway rats and $F(3, 208) = 14.14$, $p<0.001$ for the KM strain. There was no significant effect of sex and no significant interaction.

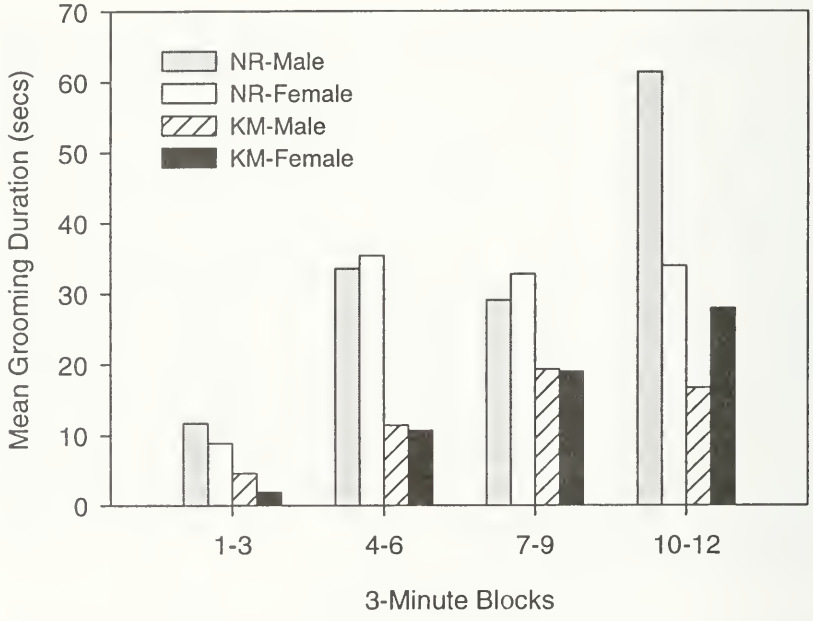

Figure 1. Mean time spent grooming by males and females of the NR and KM strains of rats over the 12 minute observation period.

Grooming was minimal in the first three minutes of the test, and during this period other activities occurred at their maximal value. Table 1 compares activity level (mean number of squares crossed) during the first and last 3-min blocks of the 12-min open-field test. Defecation occurred mainly during initial minutes of the test.

Table 1. Mean squares crossed during first and last 3-min blocks of open field test.

Parameters	NR		KM	
	Males	Females	Males	Females
Minutes 1-3	24.04	35.42	34.77	38.81
Minutes 10-12	9.87	17.85	13.73	12.58

The distribution of grooming episodes of different durations is shown in Figure 2. It is clear that for all groups of rats most episodes of grooming were 3-sec or less in duration.

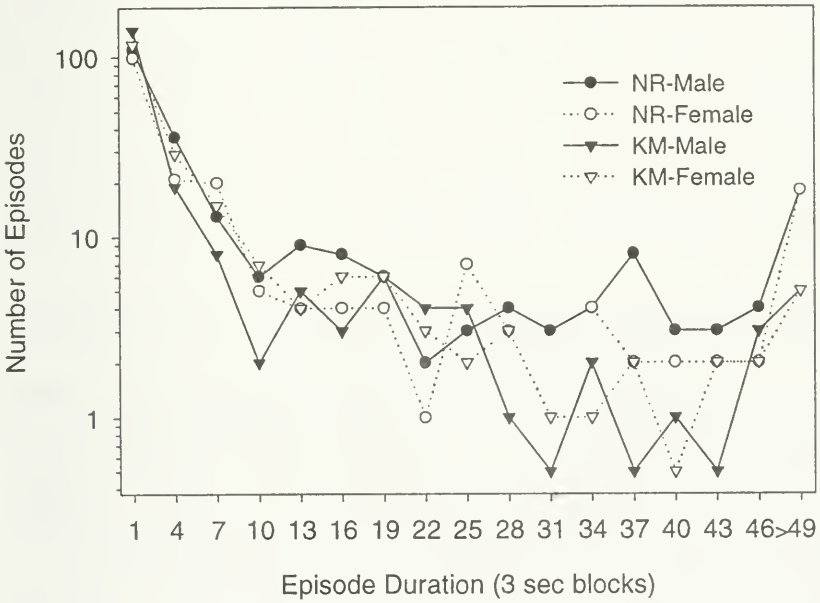

Figure 2. Number of grooming episodes (plotted on a log scale) of different duration in the two strains of rats for each sex. NR, brown Norway; KM, Krushinsky-Molodkina albino rats selectively bred for audiogenic seizure susceptibility.

The percentage of grooming episodes of different durations during each 3-minute block of the 12-minute test for the four groups of rats was also examined. There is an increase in the number of long grooming episodes late in the test. Table 2 shows the results of a

Chi-square analysis comparing frequencies of grooming episodes of different durations. A significant increase in number of episodes was observed only after the third minute. The longest grooming episodes were observed after the sixth minute in most of the rats (from 71% to 91% in different groups).

Table 2. Results of Chi-square tests of the frequencies of grooming episodes during four ranges of durations (1-3 s, 4-6 s, 10-21 s, over 21 s) when each 3-min open field period is compared with each other.

Open Field Period (mins)	Brown Norway Rats				KM Rats			
	Males		Females		Males		Females	
	χ^2	p	χ^2	p	χ^2	p	χ^2	p
1-3 & 4-6	1.86	n.s.	7.28	n.s.	7.86	<.05	5.54	n.s.
1-3 & 7-9	4.04	n.s.	13.97	<.005	8.21	<.05	9.72	<.025
1-3 & 10-12	6.70	n.s.	8.63	<.05	8.70	<.05	8.14	<.05
4-6 & 7-9	1.80	n.s.	5.82	n.s.	8.01	<.05	1.57	n.s.
4-6 & 10-12	4.48	n.s.	1.47	n.s.	20.28	<.001	5.08	n.s.
7-9 &10-12	6.73	n.s.	1.94	n.s.	6.51	n.s.	8.85	<.05

Strain and sex differences in grooming behavior

Table 3 shows performance on other behavioral measures for the total observation period (12 min). There were strain differences in some open field parameters. A two-way repeated measures ANOVA (strain x sex, 12 min observations) revealed significant strain effects in rearing ($F=12.7$, $p<.001$), defecation ($F=10.8$, $p<.002$), total duration ($F=44.1$, $p<.001$) and maximum value of grooming ($F=29.8$, $p<.001$). A statistically significant effect for sex was obtained only for number of squares crossed ($F=8.4$, $p<.005$) and defecation ($F=11.9$, $p<.002$). The NR reared more KM rats, but their defecation scores were lower. Number of crossed squares was lowest in NR males. The scores for grooming duration and maximum values of grooming episodes in the open field were higher in Norway rats in comparison to the KM rats. On the contrary, no significant effects were found for strain and sex scores for total numbers of grooming episodes.

Table 3. Mean and (S.E.M.) behavioral patterns of Norway rats (NR) and Krushinsky-Molodlina (KM) rats in an open field over the total 12-min observation period.

Behavioral Pattern	NR Rats		KM Rats	
	Males	Females	Males	Females
N	26	26	27	27
No. of Squares Crossed	68.1 (5.3)	101.5 (7.6)	88.7 (7.4)	97.9 (9.1)
Rearing	25.6 (2.6)	30.6 (2.5)	20.9 (2.6)	19.3 (1.9)
No. of Fecal Boli	3.9 (0.5)	3.4 (0.5)	8.0 (0.8)	3.7 (0.7)
Grooming: Total Duration	136.4 (13.6)	111.1 (11.6)	54.0 (5.2)	59.6 (7.6)
Grooming: Maximum Value	69.7 (7.0)	60.5 (7.7)	34.7 (4.3)	31.8 (4.1)
No. of Episodes	9.4 (1.0)	7.6 (0.8)	7.8 (0.8)	7.6 (0.8)

Table 4. Results of t-tests of strain and sex differences in total grooming durations for Norway rats (NR) and Krushinsky-Molodkina rats (MK) in an open field over successive 3-min periods.

Period (mins)	Strain Differences				Sex Differences			
	Males		Females		NR		KM	
	t (51)	*p*	t (51)	*p*	t (50)	*p*	t (52)	*p*
1-3	2.2	<0.04	3.2	<.004	-	n.s.	2	<.05
4-6	5	<.001	3.4	<.003	-	n.s.	-	n.s.
7-9	-	n.s.	-	n.s.	-	n.s.	-	n.s.
10-12	4.3	<.001	-	n.s.	2.3	<.022	-	n.s.

The results of t-tests of strain and sex differences in total grooming durations are shown in Table 4 (t values are given only for the significant differences). Strain differences in grooming durations

appear in the first minutes of the test, reaching a maximum at the 4^{th}- 6^{th} minute; there were additional large increases in grooming for NR males and a slight increase for KM females during the 10^{th} - 12^{th} minutes (Figure 1 and Table 4). Sex differences were observed at the 10^{th} - 12^{th} min in the Norway rats, with males' scores higher than those of the females. Similar differences were shown by the KM rats during the first test minutes.

There were significant strain differences in the distributions of grooming episodes of different durations across the open field test (Table 5). For the males, these differences were observed in all 3-min intervals except the 7^{th} - 9^{th} -min block. On the contrary, for females significant differences were found in 7^{th} - 9^{th} min period only. The strain differences in distributions of grooming episodes are associated with a greater number of prolonged episodes (22 sec and more) and with fewer of the shortest episodes (1-3 sec) in brown Norway rats. The increase in grooming activity in NR's at 4^{th} - 6^{th} min coincided with a reduction in the number of squares crossed without a decrease in rearing activity. On the contrary, the rearing scores of the KM rats were slowly decreasing.

Table 5. Strain differences in the distributions of grooming episodes across the open-field test (successive 3-min blocks and total scores).

Periods (mins)	Males		Females	
	χ^2	p	χ^2	p
1-3	11.84	<.01	7.06	n.s.
4-6	13.1	<.005	4.34	n.s.
7-9	0.72	n.s.	16.23	<.001
10-12	17.67	<.001	0.8	n.s.
Total:1-12	25.42	<.001	8.97	<.05

DISCUSSION

Grooming by rats in the open field has not been investigated as much as other behaviors such as walking, rearing, and defecation (Walsh & Cummins, 1976). Moreover, scant information on grooming in wild Norway rat and especially Krushinsky-Molodkina rats makes comparison of our results with those of other authors difficult. The

present results confirm strain differences in grooming performance in rats — our data on grooming duration are in agreement with those of Price and Huck (1976), who found more prolonged grooming, especially body grooming, in wild rats in comparison with domesticated Long-Evans rats. As well, Shtemberg (1982) has shown that in brown rats the number of grooming episodes is higher than in Wistar rats.

A relatively high level of emotionality in the KM rats is assumed because they showed high defecation, low rearing, and a low amount of general activity (low scores for number of squares crossed). This finding is compatible with scores for fearful brown Norway rats (Walsh & Cummins, 1976). Undoubtedly there are strain peculiarities in grooming behavior in both sexes. Increased grooming in male Norway rats has been described by Price and Huch (1976), while in the long-Evans strain sex differences were the reverse (Ivinskis, 1968; Price & Huch, 1976). In the present investigation sex differences in the grooming reaction were weaker than strain differences and practically absent in the KM rats.

Recent studies emphasize the importance of temporal profiles for the estimation of open field behavioral variables in rodents (e.g. Vadacz, Cobor & Lajtha, 1992). Our study found different effects of temporal factors on the development and the appearance of grooming. The results confirm the findings of Bindra and Spinner (1958) and Shtemberg (1982) in that the number of open field grooming episodes increased after the third minute of the test; this increase was especially prominent in brown rats (NR). Unfortunately, the cited works contain no information on the temporal characteristics of grooming episodes at various experimental stages. The present experimental results demonstrated that grooming episodes of different durations displayed different features across the course of the test. There was an increase in the number and proportion of prolonged episodes (over 21 s in duration) across the test in different rat groups. Similar changes in the temporal characteristics were also found in the course of our other test, with the last segments of the test characterized by more frequent grooming, as well as by longer latencies and durations of grooming episodes (Semiokhina & Pleskacheva, 1989). Obviously, the temporal characteristics of grooming may characterize an animal's state in the course of the experiment.

Long-duration grooming reactions are presumably caused by inhibitory processes, since they are accompanied by a decrease in the animals' motor activity. These episodes are probably of the type which Delius (1970) proposed to be associated with a brain arousal-inhibitory mechanism. The long latency for their occurrence may be due to fear.

New and frightening stimuli in the open field evoke other reactions like escape or freezing more frequently during the initial phase of a test, and these reactions compete with grooming and suppress it (Doyle & Yole, 1959; Fentress, 1973; Van Erp, Kruk, Meelis & Willekens Bramer, 1994). It is clear that short-duration episodes were not connected with the specific stage of the test and/or the decrease in locomotion. The number of grooming episodes positively correlated with rearing postures and number of crossed squares (shown in our data from the KM strain, see also Satinder, 1968; Titov & Kamensky, 1980).

It seems possible that prolonged grooming episodes have other bases and biological functions than do short-duration grooming reactions. This assumption is confirmed by recent data on a possible difference in the neurochemical basis of the factors that initiate and prolong self-grooming. Oxytocin is apparently involved in the initiation of self-grooming in rats, whereas ACTH and alpha-melanocyte-stimulating hormone prolong grooming initiated by other means, e.g. a novel environment (Van Erp, Kruk, Semple & Verbeet, 1993). Moreover, there are findings of different effects of intraventricular administrations on the temporal characteristics of grooming: ACTH prolonged grooming, without changing the number of episodes, whereas beta-endorphins increased the number of episodes (Gispen & Isaacson, 1981). Obviously, a more detailed investigation of the temporal characteristics of natural grooming, as well as the effects of various drugs on grooming, should make it possible elucidate the mechanisms of grooming, especially the possibility that it is a protective response in stressful situations.

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TEMPORAL PATTERNING OF ORAL STEREOTYPIES IN RESTRICTED-FED FOWLS: 1. INVESTIGATIONS WITH A SINGLE DAILY MEAL

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ABSTRACT: In two experiments, 24 immature female broiler breeder fowls housed in two 12-cage battery units in identical rooms received a single daily ration which they ate in 10 min, according to a programme of food restriction. From regular 15-min videorecordings, measurements were made of times spent in mutually exclusive activities (sitting, standing, head out, pacing, preening, object pecking, drinker activity). In Experiment 1, feeding time was 09.00 h in one room and 13.00 h in the other, and all birds were videorecorded in every hour of the (14-h) photoperiod on two alternate days. Differences in behaviour before and after feeding were independent of feeding time. In both rooms, head out and pacing increased before feeding, and object pecking and drinker activity (oral stereotypies) commenced immediately afterwards and then declined. Individual variation in the oral stereotypies was significant, and individuals' mean levels of both stereotypies together were consistent on the two days, but their hourly patterns were less so. Experiment 2 tested the notion of homeostatic control of oral stereotypies, by feeding all birds at 09.00 h and measuring their responses to removal of drinkers and empty feeders (main targets of the stereotypies) for either 0, 1.5 or 3 h before 15.00 h. Each cage tier received each treatment once, over three alternate days when all birds were recorded on video between 12.00 and 18.00 h (lights off). During removal of feeders and drinkers, partial suppression of object pecking and total suppression of drinker activity were balanced by corresponding increases in sitting, head out and preening. After the return of feeders and drinkers, preening declined and both stereotypies showed evidence of post-inhibitory rebound, but there was no difference between 1.5 and 3 h removal treatments. The results concur with earlier evidence indicating that preening can substitute with oral stereotypies, and it is suggested they may demonstrate homeostasis in total (substitutable) oral activity over the whole test. Conceivably, homeostasis of arousal may underlie changes in broiler breeder behaviour before and after feeding time.

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INTRODUCTION

In commercial conditions, parent stock (breeders) of meat-type chickens (broilers) are fed on restricted rations during the growing period in order to limit body weight at sexual maturity, and thereby improve health and fertility (Hocking et al., 1989). Birds fed on the recommended rations, which are provided once a day and eaten in <15 min, eat only a third as much as they would with free access to food, and are highly motivated to feed at all times (Savory et al., 1993). They are more active than ad libitum-fed control birds, and show increased pacing before feeding time and increased drinking and pecking at non-food objects afterwards. Their expression of these activities is often stereotyped in form and is correlated positively with the level of food restriction imposed (Kostal et al., 1992; Savory et al., 1992; Savory & Maros, 1993). Similar behavioural responses have been studied in breeding pigs, which are also subject to routine chronic food restriction (e.g. Appleby & Lawrence, 1987; Rushen, 1985; Terlouw et al., 1991).

When restricted-fed broiler breeders are housed individually in cages, they show oral stereotypies in the post-feeding period directed towards their drinker, empty feeder and parts of the cage (Kostal & Savory, 1994). Two further experiments with caged restricted-fed birds are reported here. In the first, two groups were studied which differed in the time their daily meal was provided, to see whether differences in behaviour before and after feeding are independent of feeding time. This was found with restricted-fed pigeons, whose peak of spot pecking after feeding remained the same when feeding time was shifted by 12 h (Palya & Zacny, 1980), and pigs' oral stereotypies also commence after feeding, whether they are given one meal a day or two (Jensen, 1988; Rushen, 1985; Terlouw et al., 1991, 1993).

Proportions of time spent performing oral stereotypies vary greatly among individual broiler breeders (Kostal et al., 1992; Kostal & Savory, 1994), and another objective here was to see how this variation is expressed in relation to time of day. From two observation days, measurements of repeatability were made of individuals' hourly patterns and mean levels of stereotyped behaviour, because the ways in which an activity varies within and between days can provide information about underlying control processes (e.g. Savory, 1993).

There was evidence from the first experiment suggesting that the stereotypies might be regulated in a homeostatic way (i.e. a steady state maintained through compensatory changes in behaviour). There is also evidence from other species that stereotypies may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983;

Dantzer et al., 1988; Jones et al., 1989). Conceivably, homeostasis of arousal (Delius, 1970; Odberg, 1993) might underlie changes in behaviour of restricted-fed animals before and after feeding time. This notion was tested in the second experiment, by measuring broiler breeders' behaviour during and after removal of the main targets of their oral stereotypies - the drinker and empty feeder. To provide evidence of homeostasis, temporary suppression of the stereotypies should be followed by "post-inhibitory rebound" (Kennedy, 1985) in those activities, and the size of the rebound should compensate for the duration of suppression. Such deprivation dependent rebounds have been demonstrated in fowls with feeding, drinking, dust-bathing and various comfort movements (Marks & Brody, 1984; Nicol, 1987; Savory, 1981; Vestergaard, 1982; Wood-Gush & Gower, 1968). They all imply some degree of homeostasis, and are consistent with models of motivation based on "psycho-hydraulics" (Lorenz, 1950) and accumulation of "action-specific energy" (Wennrich & Strauss, 1977).

The situation with broiler breeder stereotypies is complicated by the fact that they may be substitutable with another form of oral behaviour - preening. It was the only activity to increase consistently when either the drinker or empty feeder was removed in a previous study with penned birds (Kostal et al., 1992), and in another study with caged birds, drinking, pecking at the cage and preening were each dominant in different tiers of a battery system (Savory et al., 1992). It has long been recognised that effects of some motivational states on behaviour can be non-specific (Fentress, 1973), and various activities seen in frustrating situations may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983; Delius, 1970; Hutt & Hutt, 1970). For these reasons, the apparently substitutable forms of oral behaviour of restricted-fed broiler breeders could have common internal causation and consequences (Savory & Maros, 1993). In the second experiment here, neither pecking at parts of the cage nor preening could be prevented, so in analysing responses to drinker and feeder removal, attention was given to total oral behaviour, and substitution of activities during the removal periods, as well as to any rebound in behaviour afterwards.

EXPERIMENT 1: METHODS

Subjects and husbandry

Twenty four female broiler breeders (Ross 1, Ross Breeders Ltd.,

UK) were kept in a multi-unit brooder and fed ad libitum to 2 weeks of age. They were then moved to a pen and fed once a day at 09.00 h according to the restricted feeding programme in the Ross 1 Parent Stock Management Manual (authorized by UK Home Office Licence). At 8 weeks, 12 of the birds were housed individually in a 12-cage battery in a light-proof room, and these continued to be given a daily ration of "grower" pellets (150 g/kg protein and 11.0 MJ/kg metabolisable energy) at 09.00 h and will be referred to as early-fed (EF) birds. The other 12 were similarly housed in an identical battery in another identical room, and were fed thereafter on the same diet/ration at 13.00 h and will be referred to as late-fed (LF) birds. Each battery consisted of three tiers of 4 cages. Each cage measured 30 x 45 x 41 cm (w x d x h) and had solid sides, back and ceiling, and a front with vertical bars through which the bird could feed from a metal feeder and drink (ad libitum) from a 1 litre plastic container situated adjacently in a large common trough running along the outside of each tier. The drinker was filled with water daily at feeding time. Birds could see neighbours on the same tier when their heads were out of the cage fronts, but not birds on other tiers. In each room the lights were on from 06.00 to 20.00 h, and ambient temperature was maintained at 21° C.

Measurements of behaviour

At 12 weeks of age, after 4 weeks in the cages, mean body weight was 1.28 kg and the daily ration of 58 g pellets was all eaten in 10 min. The behaviour of all 12 birds in each room was recorded on videotape for 15 min (half past to quarter to) in every hour of the 14-h photoperiod on two alternate days. The recording was done remotely with equipment in a third room, and involved no disturbance to the birds.

From the videorecordings, measurements were made in each 15-min period by noting each bird's behaviour every minute from a single "on the dot" observation (Slater, 1978), according to one of seven mutually exclusive categories. These were: sitting (only); standing (only, with head inside the cage); head out (of the front of the cage while standing and often pushing against the bars); pacing; preening (nearly always while standing); object pecking (at the empty feeder or at parts of the cage); or drinker activity (drinking was interspersed with, and indistinguishable from, pecking at the water or drinker without drinking; all birds produced wet faecal droppings indicating polydipsia (Lintern-Moore, 1972)). The last two activities (but not pacing or

preening) were stereotyped in form, according to the usual definition of stereotypies (i.e. invariable, repetitive, no apparent function (Odberg, 1978)). Computer software used for this analysis was written by LK in Turbo Pascal (Borland International, USA).

Statistical analyses

Influence of feeding time (EF, LF) was assessed by seeing whether differences in behaviour before and after feeding were independent of the room used. This was done by calculating mean numbers of minutes in which different activities were observed in all the 15-min periods before feeding, and in all those after feeding, for each bird and observation day. These values were transformed by empirical logistic transform ($\log[(S+0.5)/(15-S+0.5)]$, where S is the untransformed value, Cox, 1970), to allow for lower variability at the limits of the 0-15 min scale. They were then compared by split-plot ANOVA, with birds as plots, to measure the significance of effects of bird, observation day, the difference between before and after feeding, and its interaction with feeding time/room. The results presented in Table 1 are back transformed means from this analysis, expressed as proportions of time.

To assess how consistent birds' *hourly patterns* of oral stereotypies (object pecking and drinker activity) were on the two observation days, measurements of repeatability were calculated for each hour after feeding time (expression of these activities was minimal before feeding). This was done separately for EF and LF birds, by expressing the between birds variance as a proportion of the total (between and within birds) variance (cf. Falconer, 1960), after transforming the data (number of minutes spent in object pecking and drinker activity together) by empirical logistic transform (see above). Hence, the repeatability value would be one if there was no within bird variation (between days), and zero if there was no between bird variation. Mean values of repeatability were then calculated from all the hourly values. To assess how consistent birds' *mean levels* of the stereotypies were on the two days, similar repeatability measurements were calculated from each bird's mean of the transformed hourly data used above.

To see whether individual expression of oral stereotypies was influenced by the behaviour of nearest neighbours (cf. Appleby et al., 1989; Cooper & Nicol, 1994; Palya & Zacny, 1980), each bird's overall mean time spent in object pecking and drinker activity, over all hours after feeding on both days, was correlated with that of its nearest neighbour (using the transformed data referred to above, from both (EF,

LF) rooms). With the middle two birds in each tier, that each had two neighbours, stereotypy times of these neighbours were averaged (Appleby et al., 1989).

RESULTS

Influence of feeding time

When behaviour in the hours before feeding time was compared with that afterwards, there were highly significant differences in all the activities observed (Table 1). Thus, there was more standing, head out, pacing and preening before feeding, but virtually no sitting, object pecking or drinker activity.

Table 1. Mean (n=12) proportions (%) of time spent in different activities, before (BF) and after (AF) feeding time on two days, by individually caged restricted-fed broiler breeders fed at either 09.00h (EF room) or 13.00h (LF room), and significance of effects of bird, day, feeding time (BF versus AF), and its interaction with room, from ANOVA. Analyses of variance were done with empirical logistic transformed data, and the values shown are in the observed scale (from back transformations) expressed as proportions. *P<0.05; **P<0.01; ***P<0.001; NS, not significant (P>0.05).

	EF room		LF room		Significance of effects			
Activity	BF	AF	BF	AF	Bird	Day	BF vs AF	BF vs AF x room
Sitting	0.1	5.4	0.2	2.0	NS	NS	***	**
Standing	39.1	29.1	47.6	31.3	***	NS	***	NS
Head out	25.4	13.8	26.0	12.1	***	NS	***	NS
Pacing	5.5	3.2	6.4	3.7	**	NS	***	NS
Preening	18.7	7.0	11.9	7.1	NS	NS	***	NS
'Object' pecking	1.5	21.6	1.7	25.4	***	NS	***	NS
Drinker activity	0.8	8.0	2.3	7.7	*	NS	***	NS

Head out and pacing increased as feeding time approached, while the oral stereotypies, of which object pecking was dominant, were highest immediately after feeding and declined gradually thereafter (Figure 1). The only significant interaction with feeding time/room was with sitting, which was greatly increased with EF birds in the last hour of the photoperiod. Hence, the differences in behaviour before and after feeding were relatively independent of feeding time.

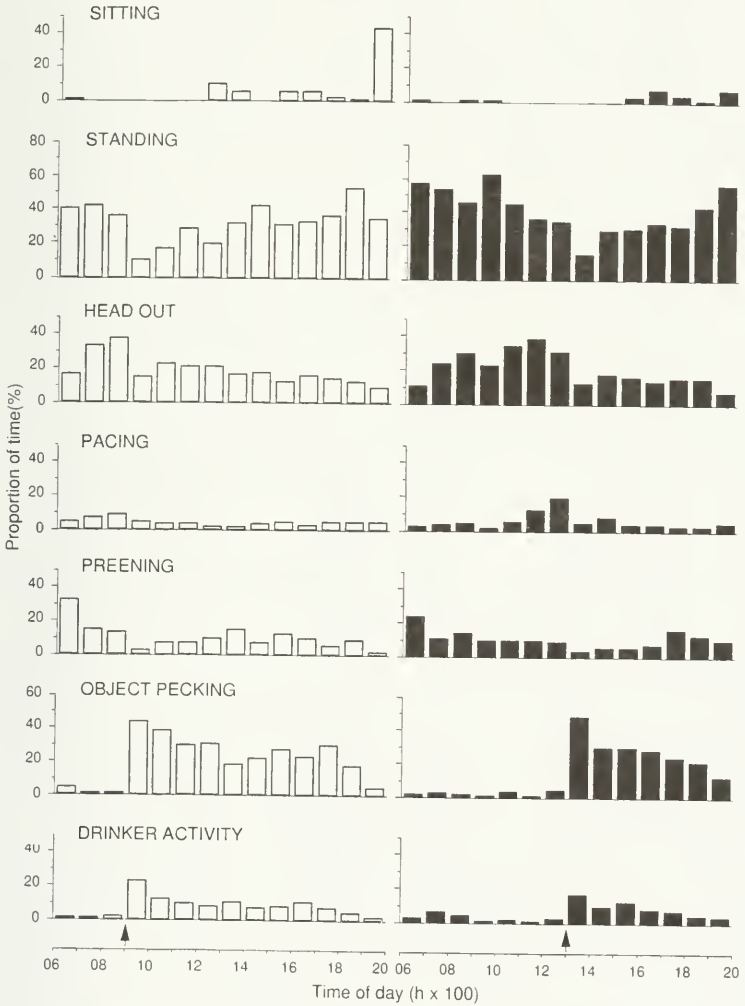

Figure 1. Mean (n=12) proportions of time spent in different activities during 15 min (half past to quarter to) in each hour of a 14-h photoperiod, from two observation days, when birds were fed at either 09.00 h (white columns, EF birds) or 13.00 h (black columns, LF birds). Arrows indicate feeding times.

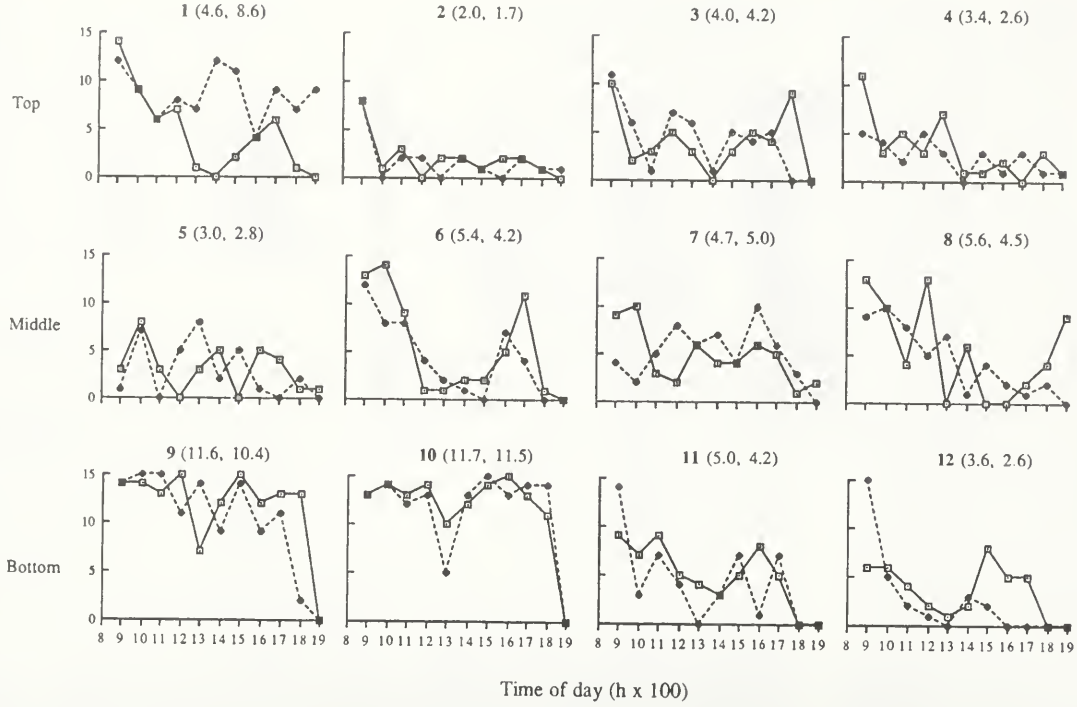

Figure 2. Total times (min) spent in stereotyped object pecking and drinker activity by each EF bird during 15 min (half past to quarter to) in each hour after feeding time (09.00 h), on day 1 (solid line) and day 2 (dashed line). Values in parenthesis after each bird number (bold) are mean times (min) spent by that bird in the two oral stereotypies, from all 15-min periods, on days 1 and 2 respectively.

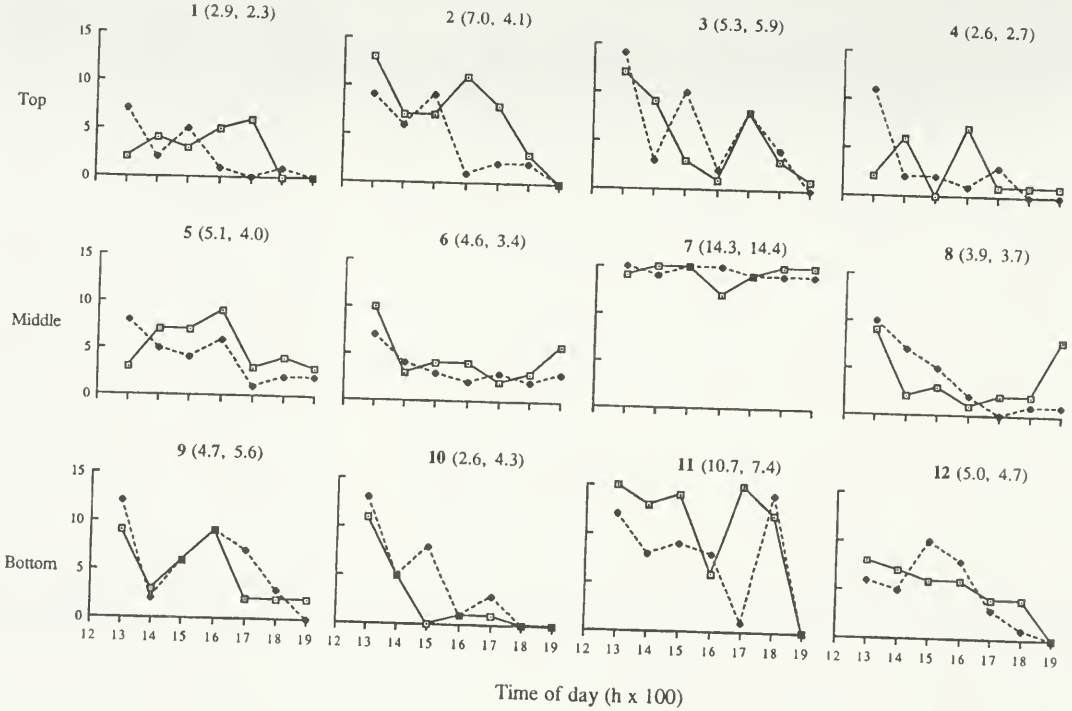

Figure 3. Total times (min) spent in stereotyped object pecking and drinker activity by each LF bird during 15 min (half past to quarter to) in each hour after feeding time (13.00 h), on day 1 (solid line) and day 2 (dashed line). Values in parenthesis after each bird number (bold) are mean times (min) spent by that bird in the two oral stereotypies, from all 15-min periods, on days 1 and 2 respectively.

Individual variation

Variation among individual birds was significant with all activities except sitting and preening (Table 1). Of the two stereotypies after feeding time, individual variation was greater with object pecking than with drinker activity, and with both EF and LF birds there were 2 birds that showed very high levels of object pecking (Table 2). When proportions of time spent in the stereotypies were added together, they ranged from 12 to 77% and 17 to 96% in EF and LF birds, respectively.

Total times (min) spent in the oral stereotypies in all 15-min periods after feeding time, on each observation day, were plotted separately for each bird (Figures 2, 3). In most instances, expression of the stereotypies was highest in the first hour after feeding and then declined. In the 4 birds with mean values of >50% (Table 2), levels remained high in either all hours (LF7) or all except the last hour (EF9, EF10, LF11). Patterns were more variable in birds with lower mean values. Secondary increases, following either low levels in the first hour or rapid initial declines, occurred at a similar time on both days in some cases (EF6, EF12, LF3, LF9).

The variability in hourly patterns was also reflected in regression coefficients (not shown) calculated between each bird's total time spent in object pecking and drinker activity in each 15 min, on each day, and the number of hours after feeding. All (48) coefficients except one were negative, reflecting the downward trends over time, but less than half (21) were significant ($P<0.05$).

Repeatability

There were no significant differences in behaviour between the two observation days (Table 1). With the oral stereotypies after feeding, measured repeatability values in different hours ranged from 0.11 to 0.77 in EF birds, and 0.23 to 0.90 in LF birds (Table 3). The mean repeatability values of 0.51 and 0.62 imply that variation in hourly patterns within birds (between days) was as great as that between birds. By contrast, repeatability values of birds' mean levels of the stereotypies were 0.90 ± SE 0.06 with both EF and LF birds. Thus, mean levels at which stereotypies were expressed (over all hours after feeding time) were much more consistent within birds than between birds.

Table 2. Frequency distributions of individual birds' mean proportions of time spent in object pecking and drinker directed activity after feeding time, when fed at either 09.00h (EF, n=12) or 13.00h (LF, n=12).

Activity	Feeding time	Percent time spent performing activity					
		<10	10-20	20-30	30-40	40-50	>50
Object pecking	EF	3	4	2	1	0	2
	LF	1	5	3	1	0	2
Drinker activity	EF	8	3	1	0	0	0
	LF	7	4	1	0	0	0
Object pecking + drinker activity	EF	0	3	2	4	1	2
	LF	0	4	3	3	0	2

Table 3. Repeatability of total (empirical logistic transformed) times spent in object pecking and drinker activity on Day 1 and Day 2, in each hour after feeding time, which was either 09.00h (ER, n=12) 0r 13.00h (LF, n=12).

Time of day (hx100) →	09	10	11	12	13	14	15	16	17	18	19	Mean
EF	0.39	0.76	0.77	0.58	0.25	0.43	0.67	0.59	0.59	0.45	0.11	0.51
LF	-	-	-	-	0.50	0.70	0.62	0.54	0.23	0.90	0.85	0.62

Influence of nearest neighbours

Individual expression of oral stereotypies was not influenced by the behaviour of nearest neighbours, judging from the weak correlation ($r = 0.06$, 22 df) between times spent in the stereotypies and those of neighbours.

EXPERIMENT 2: METHODS

Subjects and husbandry

Twenty four female broiler breeders (Ross 1) were kept in a multi-unit brooder and fed ad libitum to 3 weeks of age. They were then housed individually in cages in the same two batteries in identical rooms described in Experiment 1 Methods. Lights were on from 07.00 to 19.00 h and ambient temperature was maintained at 21°C. From 3 to 8 weeks they were used in another experiment in which the daily restricted ration (same as in Experiment 1) was provided in four equal portions at either 1 or 1.5 h intervals, commencing at 09.00 h (Savory et al., submitted). At 8 weeks their diet was changed from "starter" to "grower" pellets, and thereafter they all received a single daily meal at 09.00 h, which they ate in 10 min. The time of lights off was changed to 18.00 h.

Experimental procedure

At 13 weeks of age, after 5 weeks on the new feeding and lighting regimes, Experiment 2 was done between 12.00 and 18.00 h (lights off) on three alternate days in one week. The start of testing was thus about 2.8 h after feeding ended and presumably after food-related thirst had been satisfied. There were three treatments, where the feeders and drinkers were removed at either 14.55 h (control), 13.30 h (1.5 h removal) or 12.00 h (3 h removal), and were all replaced in their original positions at 15.00 h. All four birds on a battery tier received the same treatment at the same time, and in both rooms the three treatments were applied one to each tier on each day, according to a balanced design, so that over the three days every tier received each treatment once. When a tier's feeders and drinkers were removed, the common trough in front of it was cleaned and dried to remove any water or food particles lying in it. When they were returned the feeders

remained empty and the drinkers were filled with water to about two thirds full.

On each day, the behaviour of all 12 birds in each room was recorded on videotape for every alternate 15 min, commencing at 12.05 h and ending at 17.50 h. The recording and analysis of videorecordings was done in the same way as in Experiment 1.

Statistical analyses

It was assumed that the six battery tiers in the two rooms could be regarded as independent, because all four birds on a tier received the same treatment at the same time, and they could see each other but not birds on other tiers. For the analyses, the 6-h test was divided into four 1.5-h periods (12.00-13.30, 13.30-15.00, 15.00-16.30 and 16.30-18.00 h), each containing three of the 15-min observations. There were thus two periods before feeders and drinkers were returned at 15.00 h, and two afterwards. Within each of these periods were calculated the total numbers of minutes in which each activity was seen on each tier with each treatment (4 birds x 3 x 15 min=180 maximum). These values were transformed by empirical logistic transform, and then compared by split-plot ANOVA, with tiers as plots, to measure the significance of effects of treatment, time period, and their interaction. This was done with each of the seven activities, and also with combinations of both oral stereotypies (object pecking plus drinker activity) and total oral activity (the stereotypies plus preening). The results presented in Table 4 are back transformed means, expressed as proportions of time.

Overall mean numbers of minutes spent in each activity in each time period were expressed as proportions of time (see Results, Figure 4). Significant differences between treatments within periods were identified from the above ANOVAs, using the (treatment x time) standard errors of differences between means. This was done to identify changes in behaviour during and after feeder and drinker removal. A separate analysis was done with drinker activity because it was totally precluded for either 0, 1.5 or 3.0 h, and hence, unlike other activities, was not balanced across treatments. It was analysed by "residual maximum likelihood" tests (Welham & Thompson, 1992), to compare treatment means within the two periods after return of feeders and drinkers.

RESULTS

Treatment effects over the 6-h test

The only significant ($P<0.05$) effects of experimental treatment over the whole 6-h test were with sitting and drinker activity (Table 4). Thus, as the duration of feeder and drinker removal increased, sitting increased and drinker activity (and total stereotypy) decreased. Preening and object pecking did not differ between treatments, nor did total oral activity. There were significant effects of time period on all activities except pacing, and significant interactions between treatment and time with all activities except standing and pacing.

Table 4. Overall mean (n=6) proportions of time spent in different activities, in all time periods (12.00 to 18.00 h), by individually caged restricted-fed broiler breeders whose feeder and drinker were removed for either 0, 1.5 or 3 h, and significance of effects of treatment, time period, and their interaction, from ANOVA. Analyses of variance were done with empirical logistic transformed data, and the values shown are in the observed scale (from back transformations), expressed as proportions. [1]Object pecking + drinker activity. [2]Object pecking + drinker activity + preening. Within rows, means with different superscript are significantly different. *P<0.05; **P<0.01; ***P<0.001; NS, not significant (P>0.05).

	Duration of feeder and drinker removal			Significance of effects		
Activity	0 h	1½ h	3 h	Treat-ment	Time period	Treatment x Time
Sitting	0.1^{a}	0.3^{ab}	0.9^{b}	**	***	***
Standing	33.3	32.1	30.2	NS	*	NS
Head out	14.0	13.3	17.5	NS	***	*
Pacing	4.8	4.5	4.5	NS	NS	NS
Preening	15.8	14.7	14.5	NS	***	*
Object pecking	11.1	12.8	10.3	NS	***	**
Drinker activity	15.1^{a}	6.0^{b}	2.3^{c}	***	***	***
Total stereotypy[1]	27.5^{a}	23.1^{ab}	17.0^{b}	*	***	***
Total oral activity[2]	45.1	44.1	40.1	NS	***	***

Differences in behaviour during removal of feeders and drinkers

Feeder and drinker removal totally precluded drinker activity but not object pecking, some of which continued to be directed at the common trough in front of the cages. Object pecking was not suppressed significantly by removal of the empty feeder in the first time period (t=1.32, comparing 3 h removal with the control treatment in the same period by ANOVA, all t values have 45 degrees of freedom, P=0.05 when t=2.01), but it was in the second period with both the 1.5 h (t=2.77) and 3 h (t=2.46) removal treatments (Figure 4).

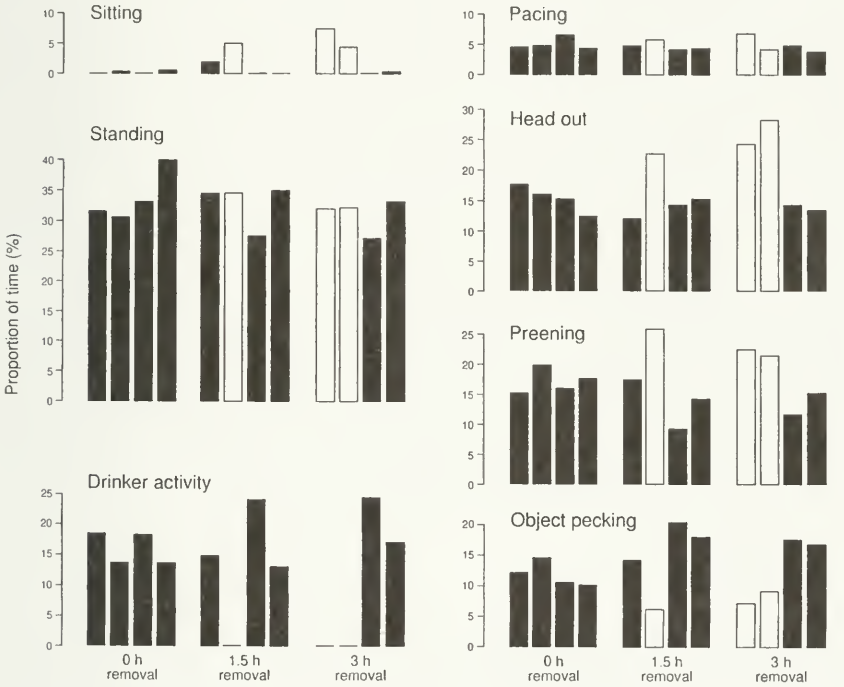

Figure 4. Mean (n=6) proportions of time spent in different activities during alternate 15 min in four time periods (12.00-13.30, 13.30-15.00, 15.00-16.30, 16.30-18.00 h), when feeders and drinkers were removed for either 0, 1.5 or 3 h before 15.00 h. White columns indicate the periods when feeders and drinkers were absent.

Sitting increased in the first period with the 3 h treatment (t=5.40), and in the second period with 1.5 h (t=2.87) and 3 h (t=3.31) removal. Head out of the front of the cage did not increase in the first period with 3 h removal (t=1.48), but did in the second period with 1.5 h (t=2.03) and 3 h (t=3.03). Preening increased in the first period with 3 h

removal (t=2.05), but not in the second period with either 1.5 h (t=1.20) or 3 h (t=0.40) treatments. One bird showed high levels of preening most of the time, directed at the same part of its body, and this was the first instance in our work with broiler breeders where the preening observed was unambiguously stereotyped. There were no other significant changes during feeder and drinker removal.

Differences in behaviour after return of feeders and drinkers

In the two periods after return of feeders and drinkers, there were no differences between treatments in either sitting, standing, head out, or pacing. Compared with the control treatment in the same period, preening was reduced with the 1.5 and 3 h removal treatments in the third (t=2.26 and 2.33) but not the fourth (t=0.90 and 1.52) period. Increased object pecking in both periods (Figure 4) was significant only with the 1.5 h treatment in the third period (t=2.04, other t values 1.62, 1.94, 1.29). From the residual maximum likelihood tests, drinker activity with both 1.5 and 3 h treatments increased significantly ($P<0.01$) in the third period ($c^2=6.80$ and 7.38, respectively, with 1 degree of freedom), but neither differed from the control treatment in the fourth period ($c^2=0.11$ and 2.11). When object pecking and drinker activity were considered together, they increased with 1.5 and 3 h treatments in the third (t=2.31 and 1.98) but not the fourth (t=1.17 and 1.47) period. There was no difference in these activities between the 1.5 and 3 h treatments in either period.

DISCUSSION

When results in Experiment 1 from caged restricted-fed broiler breeders are compared with those obtained previously from grouped birds kept in pens (Kostal et al., 1992; Savory & Maros, 1993), times spent sitting (the only index of consistent inactivity) were similarly low in both environments, reflecting a positive correlation between general activity and the level of food restriction imposed (Savory & Maros, 1993; Savory et al., 1996). Times spent in preening and other forms of oral behaviour were also broadly similar, but penned birds showed less standing and more pacing than caged birds. The increases before feeding in pacing (in pens and cages) and head out behaviour (some of which may represent forward movement blocked by the cage front) presumably reflect anticipation of food delivery.

The fact that object pecking and drinker activity were minimal before and maximal immediately after a regular meal, with both EF and LF birds (Figure 1), indicates that such stereotypies are stimulated by food consumption, regardless of time of day. This was also evident from similar findings in restricted-fed pigeons, when their daily meal was shifted by 12 h (Palya & Zacny, 1980), and restricted-fed sows given one meal a day or two (Jensen, 1988; Rushen, 1985; Terlouw et al., 1991, 1993). The oral stereotypies of pigs (mainly chain manipulation and excessive drinking) were elicited specifically by ingestion of food, and not by exposure to a loud novel sound (Terlouw et al., 1993). It has been suggested that they represent persistence of (unfulfilled) foraging behaviour after all food is eaten (Lawrence & Terlouw, 1993; Terlouw et al., 1993). Feeding activity is presumably reinforced by ingestion of food, and may continue in apparently inappropriate form in the absence of cues normally associated with satiety. This idea is based on a model proposed by Hughes & Duncan (1988), in which an animal's behaviour gets into a "closed loop" when it does not have appropriate functional consequences, or does not have them soon enough.

Oral stereotypies of broiler breeders may be similarly explained. Object pecking was most commonly directed at the inside of the empty feeder, and presumably arose through birds continuing to peck at food particles remaining after they had eaten their ration. It can therefore be regarded as an extension of normal feeding, and its development into a stereotypy may be due at least partly to continued presence of visible particles too small to grasp. Drinker activity could also be an integral part of extended feeding behaviour, because, in unrestricted fowls, food and water consumption are correlated (Savory, 1978) and most drinking occurs immediately before, during or after spontaneous meals (Yeomans, 1987). While some of the drinking after the daily meal (Figure 1) presumably reflects normal food-related thirst (Toates, 1978), each bird's consumption of most of its daily 1 litre water supply (reflected by very wet faecal droppings) greatly exceeded the 114 ml that would be expected with (unrestricted) daily food intake of 58 g (Savory, 1978). Such excessive drinking may induce oropharyngeal and gastric stimulation additional to that provided by consumption of the meal (Terlouw et al., 1993). Mean hourly levels of object pecking and drinker activity declined in parallel after feeding (Figure 1), and were correlated ($P<0.01$) in both EF and LF birds. This indicates further that they are closely linked, that they may have common cause and function (Savory & Maros, 1993), and hence that it was justifiable

to sum them here for assessment of individual variation.

Stereotypies and adjunctive behaviours have been assumed by some to reflect increased arousal (as defined by Delius, 1970) associated with frustration of specific motivational state(s), or with non-specific arousing stimuli (Berkson & Mason, 1964; Dantzer, 1986; Fentress, 1973; Killeen et al., 1978; Odberg, 1978). This assumption remains contentious (Lawrence & Terlouw, 1993) because of a lack of conclusive physiological evidence to support it. Nevertheless, it is possible that activities (mainly locomotor) that increase before anticipated mealtimes (Evans, 1971; Kostal et al., 1992; Mason, 1994; Mistlberger & Rusak, 1987; Figure 1 this paper), and those (mainly oral) that commence after feeding and then decline (Kostal et al., 1992; Jensen, 1988; Palya & Zacny, 1980; Rushen, 1985; Terlouw et al., 1991, 1993; Figure 1 this paper), reflect increasing and decreasing arousal, respectively.

Increasing arousal before a regular meal would presumably reflect anticipation, but decreasing arousal afterwards could be due to several factors. First, anticipation has ceased; second, an assumed increase in arousal caused by delivery of food may decay after feeding has ended (Killeen et al., 1978; Van der Kooy & Hogan, 1978); third, stereotypies themselves may have de-arousing consequences (Brett & Levine, 1979; Dantzer & Mormede, 1983; Dantzer et al., 1988; Hutt & Hutt, 1970). Stereotypies could thus be related to arousal in a homeostatic way (Delius, 1970; Odberg, 1993), being both stimulated by it and reducing it, just as feeding is related to hunger in unrestricted animals.

Two findings in Experiment 1 may support the notion of homeostatic control. First, individual birds' mean levels of the oral stereotypies (over all hours after feeding) were consistent on two observation days, whereas their hourly patterns were less so (Table 3). Similar consistency in stereotyped pecking over (four) days has also been found with laying hens (Blokhuis et al., 1993). Second, the secondary increases in stereotypies of some birds (e.g. EF6, EF12, LF3, LF9, Figures 2, 3) showed no evidence of extraneous causation, and might instead have been compensatory (the data from EF12 suggest different levels of compensation on the two days).

In Experiment 2, intended to test this homeostasis hypothesis, feeder and drinker removal in the first half of the 6-h test caused the overall mean proportion of time spent then in both oral stereotypies together to fall from 29% to 8% (from values in Figure 4). This reduction was balanced by corresponding increases in sitting (1% to 6%), head out (16% to 25%) and preening (17% to 23%), which were

similar in magnitude. After return of the feeders and drinkers, the only significant effects of the removal treatments were with preening, which decreased in the third period, and the two oral stereotypies, which increased in the third period. The increase then in the mean proportion of time spent in both stereotypies together, from 29% to 43%, was greater than the corresponding decrease in preening (16% to 10%). There were no differences between effects of the 1.5 and 3 h removal treatments in the last two periods.

Preening was thus the only activity which showed significant changes, both during and after feeder and drinker removal, that were opposite to those shown by object pecking and drinker activity. This concurs with previous evidence indicating that preening can substitute with oral stereotypies in the post-feeding context (Kostal et al., 1992; Savory et al., 1992), although the results here show that this substitution may only be partial. The results also appear to demonstrate post-inhibitory rebounds in both object pecking and drinker activity, which may be the first such evidence with any stereotyped behaviour. It could be argued that some of the rebound in drinker activity may reflect physiological thirst due to water deprivation. This seems unlikely because, at moderate ambient temperatures, physiological thirst depends mainly on food intake (Savory, 1978, 1986; Toates, 1978), most drinking is closely associated with mealtimes (Yeomans, 1987), and testing here started 2.8 h after feeding had ended. Also, the commercial practice of removing the water supply from broiler breeders a few hours after feeding, to prevent soiling of floor litter, was found to have no effect on physiological indices of stress (Hocking et al., 1993).

The problem for the homeostasis hypothesis is that the size of the rebounds here did not reflect the duration of feeder and drinker removal, as predicted in the Introduction. This may not be serious, however, if preening, object pecking and drinker activity are substitutable in terms of their internal consequences (Savory & Maros, 1993). Thus, although drinker activity was reduced over the whole 6-h test with 1.5 and 3 h removal of feeders and drinkers, compared with 0 h, there were no significant differences between the three treatments with preening or object pecking, or with total oral activity (Table 4). It can therefore be argued that, instead of demonstrating homeostatic compensation in the two stereotypies after the return of feeders and drinkers, these results may demonstrate homeostasis in total (substitutable) oral activity over the whole test. Hence, they could be consistent with a working hypothesis that homeostasis of arousal

underlies changes in broiler breeder behaviour before and after feeding time.

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TEMPORAL PATTERNING OF ORAL STEREOTYPIES IN RESTRICTED-FED FOWLS: 2. INFLUENCE OF MEAL FREQUENCY AND MEAL SIZE

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ABSTRACT: Expression of oral stereotypies directed at the drinker (drinking) and empty feeder (pecking), by young, caged, restricted-fed broiler breeder fowls, was investigated in three experiments in which either the frequency of feeding or meal size was varied. Behaviour was measured from regular 15-min videorecordings. In Experiment 1, birds were provided with either one (1A), two (1B) or four (1C) hourly meals of 5 g in the morning, and a single balance meal in the afternoon. Treatment 1C caused increases in drinking and pecking, compared with 1A and 1B, but effects of meal number and the total weight of food eaten during testing were indistinguishable. In Experiment 2, birds were provided with four meals of equal size in the morning, at either 1.5, 1 or 0.5 hr intervals, with a balance meal in the afternoon in the first week only. There was no difference among these treatments in drinking or pecking at any time, and neither stereotypy responded to variation in inter-feeding interval length in the ways predicted by two alternative theoretical models, constructed for adjunctive behaviours. Additional information from Experiment 1, and a comparison between Experiments 1 and 2, indicated that both stereotypies were correlated positively with meal size and/or the total amount eaten during testing. In Experiment 3, birds were provided with two meals (only) of unequal size at 09.00 and 12.00 h, and were conditioned to receiving either the large meal (32 g) first, the small meal (8 g) first, or large and small meals in random order. The main finding was that pecking declined from the first to the third hour after the small meal only when the small meal came first, and did not do so after the large meal. This suggests that the rate at which stereotyped pecking declines after eating may depend on the amount that is eaten.

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INTRODUCTION

Growing parent stock (breeders) of meat-type chickens (broilers) are routinely fed on restricted rations in order to limit body weight at sexual maturity, and thereby improve health and fertility (Hocking et al., 1989). Typically, they eat only a third as much as they would with free access to food, and are highly motivated to feed at all times (Savory et al., 1993). They are more active than ad libitum-fed control birds, and show increased pacing before a single daily meal and increased drinking and pecking at non-food objects afterwards. Their expression of these activities is often stereotyped in form (i.e. invariable, repetitive, no apparent function; Odberg, 1978) and is correlated positively with the level of restriction imposed. The oral stereotypies have been interpreted in terms of frustration of feeding motivation (Kostal et al., 1992; Savory & Maros, 1993), and persistence of unfulfilled foraging behaviour (Lawrence & Terlouw, 1993; Savory & Kostal, submitted).

Abnormal stereotypic behaviours are also shown by hungry animals exposed to more frequent intermittent feeding. Such "schedule-induced" activities can be categorised according to their temporal location in inter-feeding intervals. Thus, interim, or adjunctive, activities occur at the beginning of each interval, and (anticipatory) terminal activities near the end (Anderson & Shettleworth, 1977; Staddon & Simmelhag, 1971; Staddon, 1977). Adjunctive activities are subject to greater individual variation (Staddon & Simmelhag, 1971), and can be explained neither in terms of physiological deficit, nor as a "superstitious" result of their adventitious pairing with food delivery (Falk, 1961, 1966, 1971). A bitonic (inverted U) relationship between their rate of occurrence and inter-feeding interval length was first reported for schedule-induced polydipsia in rats (Falk, 1966), and is considered to be a common property of these activities (Bond, 1973; Allen & Kenshalo, 1976; Jozsvai & Keehn, 1990; Robinson et al., 1990).

Killeen et al. (1978) argued that expression of adjunctive behaviours is raised to supernormal levels by "excessive" arousal (as defined by Delius, 1970) generated by periodic delivery of food or other incentives. Each incentive activates a small amount of arousal which decays exponentially over time. If the interval separating successive incentives is short enough, the arousal accumulates, building to an asymptotic level which depends on the size of the arousal increments, their rate of decay, and the interval between them.

According to this ("Killeen") model, the asymptotic level of arousal (and rate of occurrence of adjunctive behaviours) increases as the inter-feeding interval decreases. Hence, the relationship between the level of adjunctive behaviour and inter-feeding interval according to the Killeen model is fundamentally different to the bitonic function referred to above (Tuyttens, 1994).

The purpose of the present study was to investigate effects of different feeding schedules on drinker and feeder directed oral stereotypies in caged restricted-fed broiler breeders (Kostal & Savory, 1994; Savory & Kostal submitted), and to see whether expression of these activities varies in the ways predicted by the Killeen model or the bitonic function for adjunctive behaviours. One experiment examined the effect of different numbers of food deliveries, with a constant inter-feeding interval, and another investigated the effect of different intervals between a fixed number of meals. Comparison between these trials indicated a specific effect of the quantity of food eaten during testing. Influence of meal size on the stereotypies was therefore examined in a third experiment, in which possible effects of anticipation of, and change from, expected meal size were also considered. Crespi (1942) reported so-called "elation" and "depression" effects on locomotor behaviour in rats given food "incentives" that were larger or smaller than expected.

EXPERIMENT 1: METHODS

Subjects and husbandry

Thirty six female broiler breeder chicks (Ross 1, Ross Breeders Ltd., UK) were kept in a multi-unit brooder until 25 days of age, with ad libitum supplies of water and a conventional "starter" mash diet (200 g/kg protein and 11.5 MJ/kg metabolisable energy).

At 25 days they were divided randomly into three groups of 12 (IA, IB, IC) and housed individually in identical batteries in three identical light-proof rooms. Each battery consisted of three tiers of 4 cages. Each cage measured 30 x 45 x 41 cm (w x d x h) and had solid sides, back and ceiling, and a front with vertical bars through which the bird could feed from a plastic container and drink (ad libitum) from a 1 litre plastic container situated adjacently outside the cage. Birds could see neighbours on the same tier when their heads were out of the front of the cage, but not birds on other tiers. In each room the lights were on

from 07.00 to 19.00 h, ambient temperature was maintained at 21°C, and white noise minimised any disturbance from extraneous sounds.

Procedure

After the move to cages, all birds were deprived of food for two days to increase their feeding motivation. Thereafter they were fed on weighed rations of the starter diet in pellet form (3 mm diameter), according to the restricted feeding programme in the Ross 1 Parent Stock Management Manual (authorized by UK Home Office Licence). Small meals (5 g per bird) were given one, two or four times per day to groups IA, IB and IC, respectively. In every case the first food delivery was at 09.00 h and the interval between successive deliveries was 1 hr. These deliveries formed only part of the daily ration, and the balance was given in a single meal at 15.00 h, so that in weeks 1, 2 and 3 of the experiment each bird's total ration was 38, 42 and 46 g/d, respectively. Water was available ad libitum, drinkers being filled daily at 09.00 h. All birds consumed the 5 g food deliveries in <10 min (Tuyttens, 1994), so subsequent pecking at the empty feeder could be considered as being non-functional.

Behaviour measurements began three days after the feeding schedules started, when birds were 31 days old. They were made on two consecutive days in each week for three weeks, by recording the behaviour of all 12 birds in each room on videotape for every alternate 15 min, commencing at 08.15 h and ending at 14.00 h. There was thus a 15 min interval in recording after every food delivery, when the 5 g meal was eaten. The recording was done remotely with equipment in a fourth room, and involved no disturbance to the birds.

From the videorecordings, measurements were made in each 15-min period by noting each bird's behaviour every minute from a single "on the dot" observation (Slater, 1978), according to one of seven mutually exclusive categories. These were: sitting (only); standing (only, with head inside the cage); head out (of the front of the cage while standing and often pushing against the bars); pacing; preening (nearly always while standing); drinking (interspersed with, and indistinguishable from, pecking at the water or drinker without drinking); pecking (at the empty feeder or parts of the cage). Although the last two activities were only truly stereotyped (according to the definition of Odberg, 1978) when they occurred at higher frequencies, they are considered in this paper as oral stereotypies. Computer software used for this analysis was written by L. Kostal in Turbo Pascal

(Borland International, USA).

Statistical analyses

Statistical analyses were carried out on mean proportions of time spent drinking and object pecking in each week, calculated for each bird from all 15-min observation periods in the two days recording. These values were $\log_e$-transformed to give approximately equal variances to all treatments, and compared by split-plot ANOVA, with birds as plots, to measure significance of effects of bird, treatment, age (week), and treatment by age interaction. Specific differences between treatments within weeks were identified from t-tests.

Mean proportions of time spent drinking and pecking were also calculated for every 15-min period separately, from the two days recording in the third week only. With each of these activities and each treatment, a Wilcoxon signed rank test was used to compare the average of the two values before 09.00 h (baseline) with every subsequent value, the value after the first food delivery with those after subsequent deliveries, and the first and last values within inter-feeding intervals. This allowed conclusions to be drawn about any change in the oral stereotypies with time of day, any progressive increase in the stereotypies after successive food deliveries (cf. the Killeen model), and any difference in the stereotypies between the beginning (interim activity) and end (terminal activity) of inter-feeding intervals. Other activities were not analysed statistically because this investigation was concerned specifically with the stereotypies.

EXPERIMENT 1: RESULTS

Overall mean proportions of time spent in different activities were 1.7% sitting, 48.7% standing, 11.4% head out, 9.6% pacing, 17.7% preening, 6.4% drinking, and 4.5% object pecking. From ANOVAs, there were significant ($p<0.001$) effects of bird with both oral stereotypies, and of treatment and age with drinking only.

Mean proportions of time spent drinking and pecking in each week are shown in Figure 1. From t-tests, time spent drinking was significantly greater ($p<0.05$ or $p<0.01$) with treatment IC (4 x 5 g meal) than with treatments IA (1 x 5 g) and IB (2 x 5 g) in all three weeks, and there was no such difference between IA and IB. With pecking, IC was greater ($p<0.05$) than IA in week 1, and greater

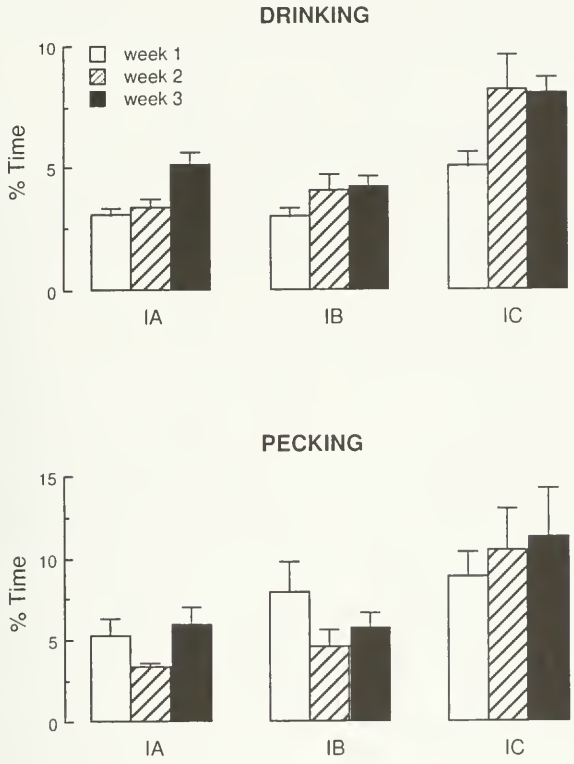

Figure 1. Mean (n=12) proportions of time spent drinking and pecking in each week of Experiment 1, by birds given either one (IA), two (IB) or four (IC) hourly meals of 5 g during testing. Vertical bars indicate standard errors.

($p<0.01$) than IA and IB in week 2, but there was no significant difference in week 3. The reason why there was no overall treatment effect with pecking (by ANOVA) was because individual variation in pecking was high. In week 3, for example, coefficients of variation (standard deviation divided by the mean) in birds' mean values were 0.57, 0.52 and 0.92 for pecking, and 0.35, 0.43 and 0.31 for drinking, with IA, IB and IC respectively.

Mean proportions of time spent drinking and pecking in each 15-min observation period in week 3 are shown in Figure 2. With treatment IA, the 09.00 h meal was followed by a significant increase in pecking (at the empty feeder) in the first 15 min, compared with the mean (baseline) value before 09.00 h. None of the subsequent pecking values differed from the baseline, and there were no such differences

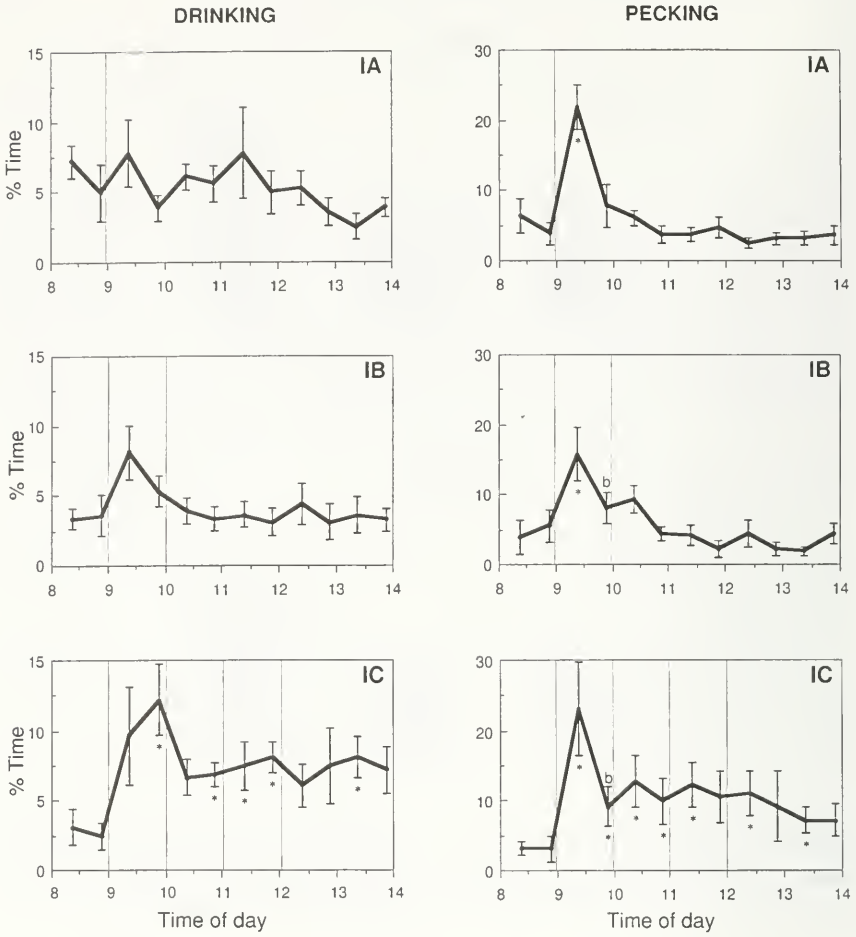

Figure 2. Mean (n=12) proportions of time spent drinking and pecking in alternate 15 min periods in the third (final) week of Experiment 1, by birds given either one (IA), two (IB) or four (IC) hourly meals of 5 g during testing. Vertical bars indicate standard errors, vertical lines from top to bottom indicate feeding times, * indicates where values differ significantly ($p<0.05$, by Wilcoxon test) from the corresponding baseline (average of the two values before 09.00 h), b indicates where values in the latter part of an inter-feeding interval differ significantly ($p<0.05$, by Wilcoxon test) from the first value in the same interval.

with drinking. With IB, pecking increased after the first (09.00 h) meal, then declined in the next 15 min, and did not increase after the second meal or subsequently. Drinking also increased after the first meal, but

not significantly so. With IC, pecking again increased after the first meal and declined in the next 15 min, and although it did not rise after the three subsequent meals, it remained higher than the baseline level. Drinking increased after the first meal, significantly so in the second 15 min, then fell after the second meal to a level that also remained higher than baseline.

For week 3 only, measurements were made of times spent drinking and pecking 45-60 min after the larger balance meal (range 18-41 g) at 15.00 h, which all birds ate in <10 min (Tuyttens, 1994). Mean proportions in the afternoon (9, 15, 11 for drinking, 31, 31, 18 for pecking, with IA, IB, IC, respectively) were nearly all greater than corresponding values 45-60 min after the first 5 g meal at 09.00 h (4, 6, 12 for drinking, 8, 8, 9 for pecking). This suggestion that larger meals may generate higher levels of the oral stereotypies was tested in Experiment 3, and was the reason for the change to no balance meal in Experiment 2. It is also possible that at least some observed effects of treatment in Experiment 1 could be associated with the total weight of food consumed between 08.15 and 14.00 h (5, 10, 20 g with IA, IB, IC), rather than with the number of food deliveries per se. This possibility was reinforced by a subsequent comparison between Experiments 1 and 2.

EXPERIMENT 2: METHODS

Subjects and husbandry

Another 36 female broiler breeder chicks were treated in exactly the same way as described for Experiment 1 until the start of Experiment 2 feeding schedules at 28 days of age.

Procedure

Experiment 2 lasted four weeks. In week 1, all three treatment groups received four 5 g meals of the pelleted food plus a single 18 g (balance) meal at 16.00 h. Groups IIA, IIB and IIC received the four 5 g meals at 1.5, 1 and 0.5 hr intervals, respectively, with the first food delivery at 09.00 h in every case. In weeks 2, 3 and 4, the complete daily ration was divided equally between these four food deliveries, with fixed meal sizes of 10.5, 11.5 and 12.5 g in the respective weeks, and there was no balance meal. The smaller (5 g) meals in week 1 were

because birds could not consume larger meals in <15 min then; and the minimum inter-meal interval was 0.5 hr to allow 15 min videorecording after all food was eaten.

Behaviour measurements began five days after the start of the feeding schedules, and they and the statistical analyses were the same as described for Experiment 1. Week 1 results were not included in the split-plot ANOVAs in order to avoid confounding any treatment by age interactions with the large change in meal size between weeks 1 and 2. The small changes in meal size between weeks 2, 3 and 4 were assumed to be insignificant for the growing birds.

EXPERIMENT 2: RESULTS

Overall mean proportions of time spent in different activities were 4.0% sitting, 35.6% standing, 15.2% head out, 8.0% pacing, 13.1% preening, 9.5% drinking, and 14.6% pecking. From ANOVAs, there were significant ($p<0.001$) effects of bird with both stereotypies, and of age with drinking only, but no effect of treatment.

Mean proportions of time spent drinking and pecking in each week are shown in Figure 3. Varying the inter-meal interval between four meals, from 1.5 (IIA) to 1 (IIB) and 0.5 hr (IIC), had no significant effect on drinking or pecking in any week. Times spent drinking and pecking were always lower in week 1, when meal size was smaller, than in the other weeks ($p<0.01$, by t-test). With all groups, drinking increased progressively (week 4>week 2, $p<0.01$), but pecking remained the same in weeks 2, 3 and 4.

Mean proportions of time spent drinking and pecking in each 15-min observation period in week 4 are shown in Figure 4. With all treatments, levels of drinking and pecking in the periods from 09.00 to 14.00 h were nearly all significantly higher than respective mean (baseline) values before 09.00 h. With treatments IIA and IIB, pecking was always higher in the first 15 min than in the subsequent 15 min period(s) within inter-feeding intervals. This was not the case with drinking, which remained consistently high in most periods after 09.00 h. Levels of drinking and pecking immediately after the first meal were not exceeded significantly after subsequent meals.

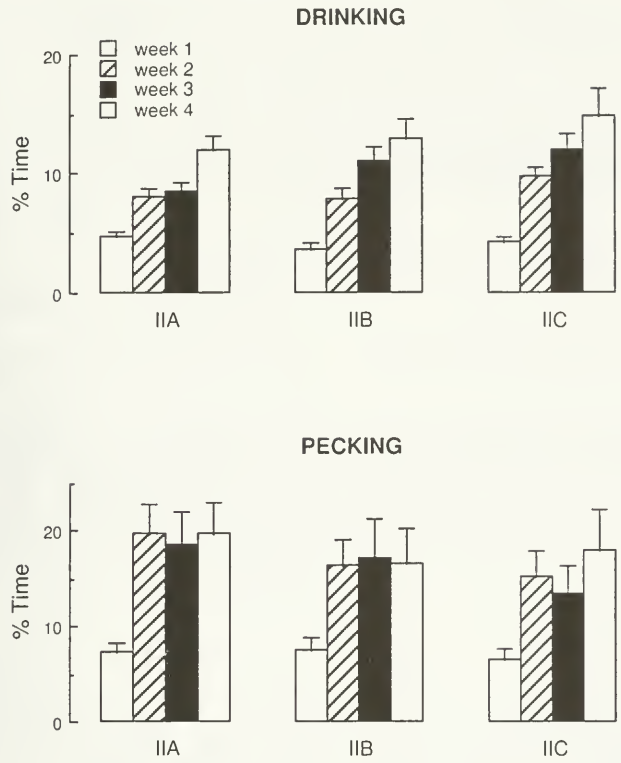

Figure 3. Mean (n=12) proportions of time spent drinking and pecking in each week of Experiment 2, by birds given four meals of equal size (5, 10.5, 11.5, 12.5 g in weeks 1, 2, 3, 4, respectively) during testing, at either 1.5 (IIA), 1 (IIB) or 0.5 hr (IIC) intervals. Vertical bars indicate standard errors.

DISCUSSION: EXPERIMENTS 1 AND 2

In Experiments 1 and 2, the feeding schedules (and ages) of treatment groups IC and IIB were the same in week 1, when both received four meals of 5 g at 1 hr intervals in the morning, and a larger (balance) meal in the afternoon. In week 2, group IC's schedule remained unchanged, but group IIB received four meals of 10.5 g at 1 hr intervals in the morning, and no meal in the afternoon. The effect of meal size and/or total quantity eaten during the test period (08.15 to 14.00 h), on drinking and pecking, can therefore be assessed from treatment by age interactions in split-plot ANOVAs, with birds as plots, IC and IIB as treatments, and weeks 1 and 2 as ages. Such treatment by age interactions were significant with both drinking ($p<0.05$) and

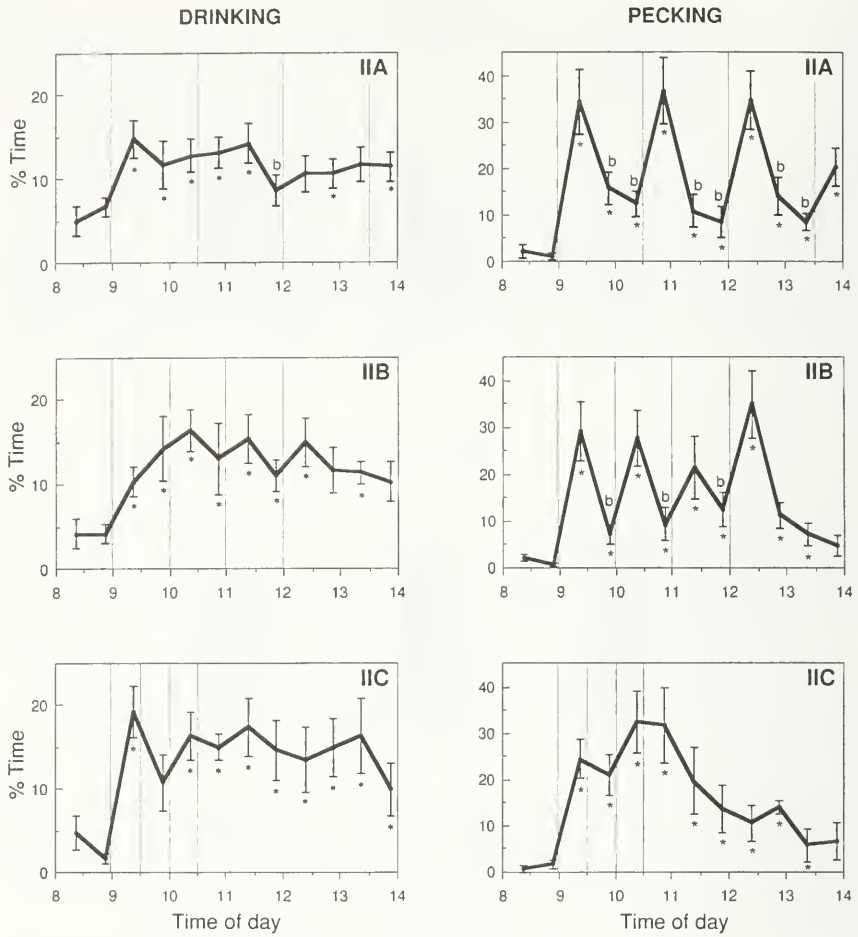

Figure 4. Mean (n=12) proportions of time spent drinking and pecking in alternate 15 min periods in the fourth (final) week of Experiment 2, by birds given four meals of 12.5 g during testing, at either 1.5 (IIA), 1 (IIB) or 0.5 hr (IIC) intervals. Vertical bars indicate standard errors, vertical lines from top to bottom indicate feeding times, * indicates where values differ significantly ($p<0.05$, by Wilcoxon test) from the corresponding baseline (average of the two values before 09.00 h), b indicates where values in the latter part of an inter-feeding interval differ significantly ($p<0.05$, by Wilcoxon test) from the first value in the same interval.

pecking ($p<0.001$), indicating that the increases in these activities from weeks 1 to 2 with treatment IIB (Figure 3) could have been associated specifically with the concomitant increase in the amount of food delivered.

This conclusion must necessarily be qualified, because groups IC and IIB were from different hatches and were not exposed to identical conditions before testing. Nevertheless, it concurs with the finding (see above) that times spent drinking and pecking in week 3 of Experiment 1 were greater after the large afternoon meal than after the first 5 g meal in the morning.

EXPERIMENT 3: METHODS

Subjects and husbandry

Twenty four female broiler breeder chicks were treated in the same way as in Experiments 1 and 2 until the start of Experiment 3 feeding schedules at 30 days of age, except that they were moved at 28 days to two 12-cage batteries (same as before) situated adjacently in the same room.

Procedure

During Experiment 3, which lasted 14 days, all birds were provided daily with 40 g of the pelleted food in two meals of unequal size (large meal 32 g, small meal 8 g) at 09.00 and 12.00 h. For the first 13 days, 8 birds (IIIA) always received the large meal first, 8 birds (IIIB) always received the small meal first, and 8 birds (IIIC) received large and small meals in different random sequences. On the final day the order of meal size in IIIA and IIIB was reversed, and IIIC remained random. Systematic distribution of treatments among cages and tiers was based on Latin squares, such that no two adjacent birds had the same treatment. The treatments were designed to separate any effects of anticipation of either a large or small meal from direct effects of meal size, and the reversed order on the final day with IIIA and IIIB was intended to test the "Crespi (1942) effect" (see Introduction) .

Behaviour measurements were made as in Experiments 1 and 2 from videorecordings of all birds in every alternate 15 min from 08.45 until 15.00 h, on each of the last four days in Experiment 3. There were thus three days (Days 1-3) when birds on treatments IIIA and IIIB were recorded on the order of meal size to which they were conditioned, and one day (Day 4) when that order was reversed. With IIIC, numbers of birds receiving large and small meals first were equal on all recording days. All birds finished their meals in <15 min, so videorecordings that

began at 09.15 and 12.15 h did so after eating had ceased.

Statistical analyses

From the 15-min observations were calculated proportions of time spent drinking and object pecking by every bird in each hour between 09.00 and 15.00 h on each day. These values were used to calculate mean proportions in the three hours after each meal (i.e. 09.15 to 12.00 h and 12.15 to 15.00 h), and changes in the proportions between the first and third hours after each meal. The mean proportions from three-hour periods were transformed by angular (arcsine root) transformation (Bartlett, 1947) before analysis, to give approximately equal variances, but this was not necessary with the changes between first and third hours. Because the experimental design was unbalanced (conditions were the same on all four days with IIIC but not with IIIA and IIIB), data were examined by "residual maximum likelihood" analysis (Patterson & Thompson, 1971), allowing for fixed effects (day(s), treatment, meal size) and random effects (bird, cage position). Specific questions concerned with meal size (see Results) were addressed by making appropriate comparisons among means, and dividing the resulting differences by their standard errors to obtain z values which were compared with the normal distribution (Wald tests).

EXPERIMENT 3: RESULTS

Overall mean proportions of time spent in different activities were 2.8% sitting, 45.7% standing, 15.5% head out, 4.1% pacing, 7.0% preening, 6.5% drinking, and 18.5% pecking. In the 15 min before the first meal at 09.00 h, mean proportions of time spent drinking and pecking were 1.3% and 4.2%, respectively.

Drinking and pecking responses in the three hours after large and small meals, with treatments IIIA, IIIB and IIIC, are shown in Figure 5. The following five questions were addressed.

1. Is any effect of meal size independent of anticipation of meal size? Considering data from IIIC only (no anticipation of meal size), the only significant effect of meal size was with the change in time spent drinking between first and third hours, which was greater after the large meal ($z = 3.12$, $p<0.01$).

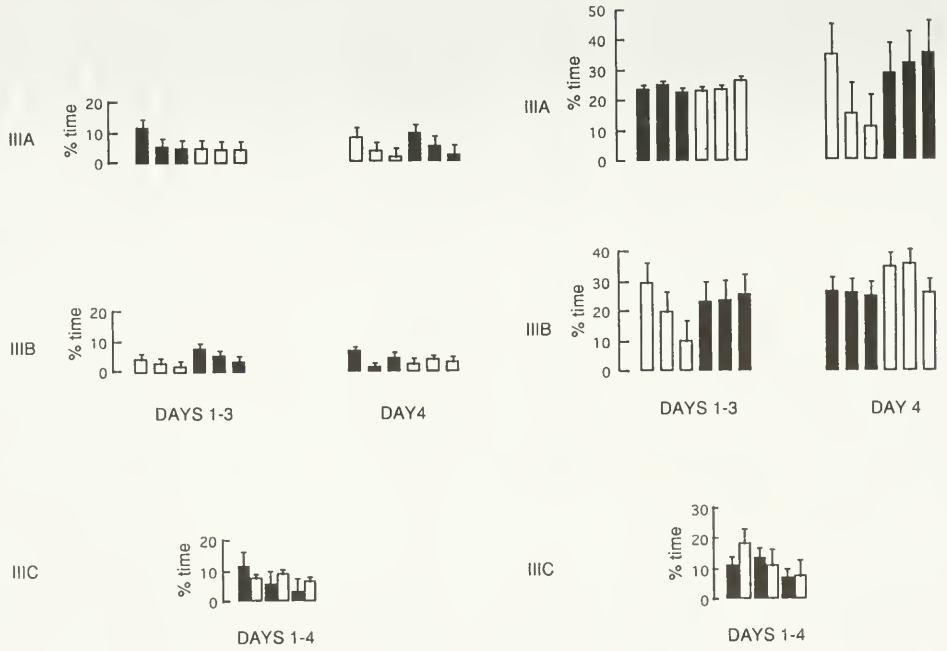

Figure 5. Mean (n=8) proportions of time spent drinking and pecking in the three hours after large (32 g, black columns) and small (8 g, white columns) meals at 09.00 and 12.00 h. On Days 1-3, (conditioned) birds received either the large meal first (IIIA), the small meal first (IIIB), or large and small meals in random sequences (IIIC). On Day 4, the order of meal size in IIIA and IIIB was reversed, and IIIC remained random. Vertical bars indicate standard errors.

2. Is any effect of meal size influenced by anticipation of meal size?
There were no significant differences between effects of meal size with IIIC and average effects of meal size with IIIA and IIIB.

3. Is there any effect of anticipation of meal size per se?
There were no significant differences between overall effects (regardless of meal size) of IIIC and average overall effects of IIIA and IIIB.

4. Is any effect of meal size influenced by order of presentation?
Comparing IIIA and IIIB, there was a significant effect of order on the difference between large and small meals in the change in time spent pecking between first and third hours (Days 1-3, $z = 2.75$, $p<0.01$; Day 4, $z = 1.81$, $p = 0.07$). Thus, with both IIIB and IIIA, there was a marked decline in pecking after the small meal only when the small meal came first (Figure 5). On Day 4, there was also a significant effect of order on the mean proportions of time spent pecking in three-hour periods ($z = 2.47$, $p<0.02$). Thus, (on Day 4 only), mean time spent pecking was greater after the second meal than after the first meal, regardless of meal size. There were no other effects of order.

5. Is any effect of meal size influenced by unexpected change in order of presentation? ("Crespi effect")
There was no significant effect of the change in order of presentation (on Day 4) on mean proportions of time spent drinking and pecking in either the first hour or all three hours after the first meal, with either the large meal (IIIA on Days 1-3 vs IIIB on Day 4) or the small one (IIIB on Days 1-3 vs IIIA on Day 4).

GENERAL DISCUSSION

The aim of Experiments 1 and 2 was to see whether the oral stereotypies of caged restricted-fed broiler breeders (drinking and object pecking) respond to variation in feeding frequency in the ways predicted by the Killeen model (Killeen et al., 1978) for adjunctive behaviours.

The results of Experiment 2, in which four meals of the same size were provided at either 0.5, 1 or 1.5 hr intervals, did not concur with these predictions. There was no difference between treatments in overall levels of either drinking or pecking during testing, and no evidence within treatments of accumulation in either stereotypy between successive food deliveries. Similarly, there was no evidence of such

accumulation in Experiment 1, when either two (IB) or four (IC) meals of the same size were provided at 1 hr intervals. There was also no evidence in Experiment 2 of the bitonic relationship between behavioural expression and inter-feeding interval length, reported by others to be characteristic of adjunctive behaviours (see Introduction).

The question arises, therefore, whether drinking and pecking stereotypies of broiler breeders, with low frequencies of feeding, are truly analogous to the adjunctive behaviours of animals with higher frequencies of feeding. Both types of behaviour do have features in common. Their level of expression is correlated positively with the degree of food restriction (Falk, 1971; Savory & Maros, 1993); they are persistent, excessive and stereotyped in some individuals; and they are rarely seen before the first food delivery (Figures 2 and 4; Kostal et al., 1992; Savory & Kostal, submitted). Drinking, however, cannot be regarded as an interim adjunctive activity here because it was not focussed immediately after feeding (Figures 2 and 4), unlike schedule-induced polydipsia (Staddon, 1977). Pecking did appear to be focussed after feeding, but only with the larger meals in Experiment 2 (Figure 4). Also, there was consistently greater individual variation in pecking than in drinking in these experiments, and this is typical of adjunctive behaviours (Staddon & Simmelhag, 1971). It is quite possible that, with more (small) meals and shorter intervals than those tested here, the oral stereotypies of broiler breeders would respond in ways predicted by the Killeen model or the bitonic function.

In Experiment 1, regular provision of four small meals in the morning (IC), together with a single balance meal in the afternoon, was associated with greater and more prolonged increases in drinking and pecking during testing (08.15 to 14.00 h) than were either of the other two treatments with fewer meals (Figure 2). One possible explanation for this is that neural elements controlling these activities become sensitised through repeated stimulation, leading to exaggeration and stereotyping of the activities (Dantzer, 1986), and this happens sooner with more meals per day. This process depends on the arousal generated by intermittent delivery of insufficient food (Cabib, 1993), and on associated increases in feeding motivation and general activity (Baumeister et al., 1964; Savory et al., 1996). The sorts of activity it affects reflect the extent to which behavioural expression is constrained or "channeled" by the environment (Lawrence & Terlouw, 1993).

However, as well as the above effect of meal number, there may have been an additional effect due to more food being eaten during testing with treatment IC (20 g) than with IA (5 g) and IB (10 g). It is

impossible here to separate effects of meal number and the amount eaten, but there is other evidence from Experiments 1 and 2 indicating that meal size and/or total amount eaten may be important (assuming a fixed level of food restriction). First, the increases in drinking and pecking from weeks 1 to 2 with treatment IIB (Figure 3) could have been caused by the concomitant increase in the amount of food delivered (inter-experimental comparison). Second, in week 3 of Experiment 1, times spent drinking and pecking after the large afternoon meal were nearly all higher than corresponding levels after the first 5 g meal in the morning (Experiment 1 Results). Third, levels of drinking and pecking were consistently high after each of four hourly meals of 12.5 g in Experiment 2 (IIB, Figure 4), but dropped after the first of four hourly meals of 5 g in Experiment 1 (IC, Figure 2).

In Experiment 3, there was no apparent effect of meal size on mean times spent drinking and pecking in three-hour periods after two meals of unequal size (large - 32 g, small - 8 g) provided at 09.00 and 12.00 h. With treatment IIIC (random order, no anticipation of meal size), the change in time spent drinking between first and third hours was greater after the large meal than after the small one (Figure 5). This may be because food-related thirst was presumably greatest in the first hour after the large meal. Another effect was with time spent pecking, which declined from the first to the third hour after the small meal only when the small meal came first (i.e. IIIB on Days 1-3 and IIIA on Day 4), and did not do so after the large meal. The results suggest that the increase in stereotyped pecking after the first meal may be relatively independent of meal size, but the rate at which pecking declines afterwards may be greater with small meals than large ones. If this effect also applies to differences in total food eaten during testing, as in Experiment 1, then it might have contributed to the more prolonged increases in drinking and pecking observed with IC (Figure 2). There also appeared to be no effects on oral stereotypies in Experiment 3 that could be attributed specifically to either anticipation of meal size or unexpected change in (anticipated) meal size (cf. Crespi, 1942).

In conclusion, the oral stereotypies of restricted-fed broiler breeders did not respond here, to variation in inter-feeding interval length, in the ways predicted by either the Killeen model or the bitonic function for adjunctive behaviours. This might have been because the minimum interval tested in Experiment 2 (0.5 hr) was too long for these predictions to be realised. Drinking and pecking levels in Experiment 1 were higher with four hourly food deliveries per day than with either two or one, but effects of meal number and the total weight eaten during

testing were indistinguishable. Results of Experiment 3 indicate that the rate at which stereotyped pecking declines after eating may depend on the amount that is eaten.

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